

Full Length Research Paper

Growth and physiological responses to water and nutrient stress in oil palm

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Accepted 11 July, 2011

The research was conducted to detect changes in growth, physiology and nutrient concentration in response to two watering regimes (well-watered and water-stress conditions) and to two nutrient regimes (with or without fertilization) of oil palm. Under stress conditions, changes in plant growth, dry matter allocation, relative water content, leaf relative conductivity, leaf N, P and K concentration are usually observed. These characteristics and related parameters were determined and the experiment results are listed as follows: (1) fertilization promoted the growth of oil palm under well-watered conditions, while under water stress conditions its effects on growth was negative. The ratio of root/shoot was increased under water stress condition; (2) relative water content and chlorophyll a/b content were gradually decreased while leaf relative conductivity was increased quickly under water and nutrient stress conditions during the experiment. It is obvious that water stress had a greater influence than nutrient stress on these parameters; (3) water and nutrient stress decreased leaf nitrogen and phosphorus concentration but increased potassium concentration; the combination of water and nutrient stress made significant effects on nitrogen and phosphorus concentration, but no significant effects on potassium concentration. Moreover, deficiency of both water and nutrients in combination had the greatest impact on changes in these traits of oil palm.

Key words: Plant growth, physiology response, nutrient concentration, water stress, nutrient stress.

INTRODUCTION

Water and nutrient deficiency are major factors limiting the productivity and geographical distribution of many species, including important agricultural crops (Conner et al., 1998; Zhang et al., 2007; Tseira and Irit, 2009; Andrews et al., 2010). Fertilization is most effective when trees are not water-stressed, and irrigation is most effective when nutrients are not scarce (Sands and Mulligan, 1990). Therefore, understanding the mechanisms of plant tolerance to water and nutrient stress is a crucial environmental research topic (Wang et al., 2009a). Generally, exposure to water or nutrient stresses triggers many common reactions in plants that lead to a decrease in the

growth rate and relative water content; change of the biomass partition and nutrient distribution. Another consequence of exposure to these stresses is the increase in root/shoot ratios and leaf relative conductivity. Numerous studies have shown that plants will respond to a large set of parallel changes in growth, and in morphological and physiological responses when the plants are exposed to water or nutrient stress environment (Chapin, 1991).

Until now, many researchers clarified numerous effects on plant growth (Ismail et al., 1994; Wang et al., 2009b), dry matter allocation (Yin et al., 2005; Mandal et al., 2006; Wu et al., 2008; Li et al., 2009; Sun et al., 2009; Gerardeaux et al., 2010), photosynthesis (Syros et al., 2004), nutrient concentration and status (Wang et al., 1998; Jose et al., 2003; Slamaa et al., 2008; Keutgen and Pawelzik, 2009). The oil palm (*Elaeis guineensis* Jacq.) is a perennial monocotyledonous plant which belongs to the

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family Arecaceae originating from West Africa. The fruit pulp and nut that provide palm and kernel oil, respectively, made oil palm a high yielding oil-producing crop (Henderson and Osborne, 2000; Corley and Tinker, 2003). At present, palm oil production is second only to that of soybean oil in terms of world vegetable oil production and the demand for palm oil is expected to increase in future (Ho et al., 2007; Yusof, 2007; Corley, 2009; Bateman et al., 2010). In order to meet the increasing demand for palm oil, an improvement in yield is required despite the large body of literature on water and nutrient stress, as the important stress of oil palm in most tropical or subtropical area.

Although some reports showed that the responses of oil palm are related to water stress (Smith, 1988; Caliman, 1992; Gawankar et al., 2003; Kallarackal et al., 2004; Henson et al., 2005; Mohd Roslan Noor, 2006; Legros et al., 2009; Omorefe and Bonaventure, 2010; Cha-um et al., 2010), or the effects of nutrient on plant growth, physiological variance and yield of oil palm (Ng, 1979; Van Kraalingena et al., 1989; Remison et al., 2000; Bah and Rahman, 2004; Taryo-Adiwigandaa et al., 2006; Anuar et al., 2008; Tan et al., 2010), to our knowledge little is known about the effects of water and nutrient stress on this plant. Therefore, there is a pressing need to know in more detail how oil palm responds and adapts to such conditions. In this work, we examined the variance of plant growth, dry matter allocation, relative water content, leaf relative conductivity, chlorophyll a/b, changes of leaf total N and P concentration were also determined.

MATERIALS AND METHODS

Plant material and experimental design

The experiment design combined two water levels [90 and 50% field water capacity (FC)] and two nutrient levels (no fertilizer supplied to the plants or irrigated with Hoagland solution to each plant every 15 days). In the well-watered treatment, the pots were rewatered to FC by replacing the amount of transpired water every second day. In the water-stressed treatments, the pots were watered to 50% of FC every second day to maintain the drought level in the soil. Therefore, four experimental treatments were conducted: +W+F and -W+F, were control treatment (90% field water capacity with applied fertilizer) and water stress treatment (50% field water capacity with applied fertilizer) respectively; while +W- F and -W- F, were nutrient stress treatment (90% field water capacity without applied fertilizer), and water and nutrient stress treatment (50% field water capacity without applied fertilizer), respectively. Water leakage from bottom of the pot and evaporation from the soil surface was prevented by enclosing all soil in plastic bags. Thereafter, pots were divided into four groups; three replicates each. The pots were randomly switched places often, so as to decrease the differences in microclimates. The seedlings were randomly sampled at 0, 30, 60, and 90 days for measuring the investigated traits.

Growth measurements

Growing plant height was measured as the distance from soil surface to upper end of the longest leave. The total leaf area was

determined by a portable laser area meter (CI-203, CID Inc., USA). Whole plants from all treatments were harvested at 0, 30, 60, and 90 days of the experiment, and divided into leaves, stems and roots. Plant samples were first dried at 120°C for 2 h, and then oven-dried at 80°C until constant weight and weighted with analytical balance. Root/shoot ratio (Rs) were then calculated.

Measurements of relative water content (RWC), leaf relative conductivity, and chlorophyll content

RWC of leaves

RWC was estimated by recording the turgid weight of fresh leaf samples by keeping them in water for 24 h, followed by drying in a hot air oven until constant weight was achieved. $RWC = (FW - DW) \times 100 / (TW - DW)$, where FW is the fresh weight, TW is the turgid weight of dehydrating samples which were enclosed in black envelope at about 25°C for 24 h and DW is the dry weight of leaves after oven-drying samples at 85°C for 24 h (Whetherley, 1950).

Leaf relative conductivity

After treatment, the fully expanded leaves were randomly selected from three seedlings per replication, and a DDS-11A Conductivity Meter was used to measure the conductivity of the solutions. The percentage of membrane damage was calculated as a relative conductance using the formula: $(C_1 - C_w) / (C_2 - C_w) \times 100$, where C_1 is the electrical conductivity value of samples at the first measurement, C_2 is the conductivity after boiling and C_w is the conductivity of deionized water. The relative conductivity was carried out according to the method described by Premachandra et al. (1991) described with little modification.

Chlorophyll content

The fresh leaves were ground in 80% acetone as quickly as possible at room temperature, and the chlorophyll (Chl) contents (Chla, Chlb and Chla/b) were determined using a spectrophotometer (SCHOTT UVLINER 9400, German) at 470, 646 and 663 nm and by the calculations described by Wellburn (1994).

Determination of nitrogen, phosphorus, and potassium content in oil palm leaves

At the end of the experiment, the leaves for the nitrogen, phosphorus, and potassium content analysis were dried at 80°C until constant weight and then ground. The dried samples were milled and subsequently digested with concentrated H_2SO_4 and H_2O_2 . The total N and its proportional concentration (N%) were analyzed with the micro-Kjeldahl method (Liang and MacKenzie, 1994). The total P was determined by using molybdate-blue colorimetric method. The calculation of phosphorus content was as described by Kitson and Melon (1944) and Hocking and Meyer (1991). Potassium from samples was determined by analyzing with a flame photometer. Potassium content was calculated as mentioned by Siddiqi and Glass (1981) and Yang and Zhou (2007).

Statistical analyses

The results presented are the mean values \pm standard errors obtained from at least three replicates. Significant differences between the treated and control plants were determined using ANOVA test ($P < 0.05$ and $P < 0.01$). Statistical analyses were conducted using the statistical soft ware package SPSS11.5 for Windows.

Table 1. The effect of watering and fertilization on plant growth and biomass partitioning.

Variable	Day	Treatment			
		CK (+W+F)	-W+F	+W-F	-W-F
Plant height	0	68.94±1.22 ^a	69.07±1.30 ^a	68.81±1.21 ^a	69.09±1.21 ^a
	30	73.50±1.34 ^a	72.40±1.33 ^a	70.00±1.25 ^{ab}	69.92±1.22 ^b
	60	77.00±2.00 ^a	72.67±1.60 ^a	72.08±1.31 ^a	71.25±1.37 ^a
	90	79.00±2.10 ^a	73.60±1.71 ^{ab}	73.13±1.35 ^{ab}	72.50±1.31 ^b
Leaf area	0	260.08±1.53 ^a	259.43±0.78 ^a	258.93±2.01 ^a	259.29±1.90 ^a
	30	303.57±2.15 ^a	269.49±1.90 ^b	295.35±0.47 ^a	265.69±1.42 ^b
	60	316.19±1.32 ^a	272.98±2.67 ^b	308.48±2.01 ^a	267.95±1.09 ^b
	90	331.18±1.91 ^a	279.53±0.69 ^b	321.12±2.36 ^a	272.05±1.37 ^c
Root/shoot ratios	0	0.19±0.41 ^a	0.19±0.47 ^a	0.19±0.43 ^a	0.19±0.56 ^a
	30	0.23±1.07 ^b	0.26±0.54 ^a	0.25±1.11 ^b	0.26±1.23 ^a
	60	0.26±1.81 ^b	0.28±3.10 ^a	0.25±1.54 ^c	0.27±1.13 ^a
	90	0.27±0.57 ^{ab}	0.34±1.43 ^a	0.26±2.21 ^b	0.29±1.03 ^a

Different letters in the columns indicate significant differences between the watering and fertilization treatments at $P < 0.05$ level.

RESULTS

Plant growth and biomass partitioning

The plant growth that was sustainably increased during the experimental period was observed. After about 3 months of continuous growth, the dry matter accumulation and allocation were significantly affected by water and nutrient stress (Table 1). With the duration of stress time, the growth rate was slower than the initial stage. At the end of the experiment, water and nutrient stress decreased both plant height and leaf area, resulting in a significant water \times nutrient interaction. Seedling grew taller in the control treatment compared to other treatments. Similarly, a significant increase in leaf area was observed for seedlings in the control treatment over the water and nutrient stress treatment.

The root : shoot ratio was mainly influenced by water treatments. More biomass was partitioned to above-ground tissue in both nutrient stress treatment and control treatment than water stress treatment, respectively. Conversely, below ground allocation was greater in the water treatment than other treatments. These distribution patterns resulted in increased root : shoot ratio for seedling grown under water stress. It is obvious that water stress had a far greater influence on root : shoot ratio than nutrient stress.

RWC, leaf relative conductivity, chlorophyll a/b

RWC, leaf relative conductivity, and chlorophyll a/b were affected by the experimental factors (Table 2). RWC, and

chlorophylla/b gradually decreased and leaf relative conductivity greatly increased under water and nutrient stress during the experimental period. The RWC was highest in the control (+W+F) treatment, but lowest in the -W-F treatments. Conversely, leaf relative conductivity was significantly higher in the water stress treatments than in the well-watered treatments. At the end of the experiment, Chlorophyll a/b was significantly influenced by water and nutrient stress. However, Chlorophyll a/b remained stable under control treatment. These results also showed that water stress had a greater influence on these traits than nutrient stress.

Nitrogen, phosphorus and potassium concentration

As shown in Table 3, at the end of the experiment, the main effects, the interaction between water and nutrient stress, was significant for leaf nitrogen and phosphorus concentration ($P < 0.05$), but had no significant effect on potassium concentration. Nitrogen, and phosphorus concentration was lower in the nutrient and nutrient-water stressed plants compared to the control plant. The highest decrease in nitrogen, phosphorus, potassium concentrations were 11.4 and 27.4%, respectively. But potassium concentration was increased under stress condition.

Relationship between physiological and biochemical parameters of oil palm seedlings

It can be seen from Table 4, that under +W+P (control)

Table 2. Effect of watering and fertilization on relative water contents, leaf relative conductivity, Chlorophyll a/b.

Variable	Day	Treatment			
		CK (+W+F)	-W+F	+W-F	-W-F
Relative water contents	0	97.74±1.33 ^a	93.72±1.30 ^a	95.70±1.31 ^a	96.84±1.34 ^a
	30	96.4±1.25 ^a	92.28±0.89 ^a	93.85±0.84 ^a	90.04±0.68 ^b
	60	96.37±1.22 ^a	84.94±0.47 ^b	85.24±0.87 ^b	75.6±0.31 ^c
	90	96.34±1.31 ^a	70.43±0.21 ^{bc}	78.78±0.46 ^b	56.55±0.09 ^c
Leaf relative conductivity	0	104.22±1.88 ^a	102.21±1.78 ^a	103.22±1.68 ^a	101.12±1.58 ^a
	30	149.87±1.88 ^c	173.2±1.91 ^a	169.29±1.85 ^{bc}	170.83±2.01 ^a
	60	151.96±1.92 ^c	593.92±2.048 ^{ab}	209.03±2.18 ^{bc}	870.62±2.58 ^a
	90	162.99±1.98 ^c	1053.25±3.68 ^a	368.25±2.44 ^{bc}	1153.99±3.88 ^a
Chlorophyll a/b	0	2.01±1.08 ^a	2.11±1.31 ^a	2.13±1.64 ^a	2.14±1.41 ^a
	30	2.00±2.12 ^a	1.81±1.41 ^a	1.83±1.54 ^a	1.78±1.03 ^b
	60	1.99±1.88 ^a	1.63±1.12 ^b	1.79±1.24 ^{ab}	1.48±0.87 ^c
	90	1.93±1.67 ^a	1.42±0.78 ^b	1.62±1.02 ^{ab}	1.21±0.47 ^c

Different letters in the columns indicate significant differences between the watering and fertilization treatments at $P < 0.05$ level.

Table 3. Effect of watering and fertilization on leaf nitrogen, phosphorus, and potassium concentration at final harvest.

Variable	Treatment			
	CK (+W+F)	-W+F	+W-F	-W-F
Nitrogen concentration (%)	1.15±0.12 ^a	1.14±0.14 ^a	0.97±0.05 ^b	0.93±0.05 ^b
Phosphorus concentration (%)	0.12±0.01 ^a	0.11±0.01 ^a	0.10±0.00 ^{ab}	0.09±0.00 ^b
Potassium concentration (%)	0.97±0.09 ^b	1.26±0.12 ^a	1.02±0.11 ^{ab}	0.99±0.11 ^b

Different letters in the columns indicate significant differences between the watering and fertilization treatments at $P < 0.05$ level.

treatment, leaf area showed a significant positive and negative correlation with relative water content and potassium concentration, respectively ($P < 0.05$). Under -W+F treatment, Chlorophyll a/b showed a positive correlation with plant height ($P < 0.05$) and leaf relative conductivity ($P < 0.01$). In addition, the correlation between plant height and leaf relative conductivity, phosphorus concentration and root/shoot ratios, relative water content and nitrogen concentration also showed significant positive correlation ($P < 0.05$). Under +W-F treatment, leaf area and phosphorus concentration, nitrogen and potassium concentrations were significantly positive and negatively correlated at the significance level, ($P < 0.01$) respectively. The positive correlation between relative water content and root/shoot ratios was also highly significant ($P < 0.05$). Under -W-F treatment, leaf area and Chlorophyll a/b, root/shoot ratios and potassium concentration were significantly positive and negatively correlated at the significance level, ($P < 0.01$) respectively, and phosphorus concentration showed a significant positive correlation with leaf area and

Chlorophyll a/b ($P < 0.05$).

DISCUSSION

Under environmental stresses, plants would change their biomass allocation between organs, and the growth rate would gradually become slow with the duration of stress time. At the end of experiment, the effects of the interaction between water and fertilization on plant height, leaf area, and dry mass accumulation (including total biomass, root, stem and leaf mass) were significant. Water and nutrient stresses suppressed growth rate, as also previously observed (Hsiao, 1973; Munns, 2002; Karageorgou et al., 2002; Stefens et al., 2005; Song et al., 2010; Weih, 2010). Judging by the variance of plant growth in Table 1, there was no significant difference between water and nutrient stress, when applied separately on plant growth. Some reports argue that water is more limiting than nutrient because the increase in growth between well-watered and water stressed with

Table 4. Relationship between parameters, plant height (pH), leaf area (LAR), R/S (root/shoot ratios), RWC (relative water content), RC (leaf relative conductivity), Chl a/b (Chlorophyll a/b), N con (nitrogen concentration), phosphorus concentration (P con), potassium concentration (K con) of oil palm seedlings grown under water and nutrient stress at final harvest.

Treatment	Correlation Coefficient									
	Traits	PH	LAR	R/S	RWC	RC	Chl a/b	N con	P con	k con
+W+F	LAR									
	R/S									
	RWC		*							
	RC									
	Chl a/b									
	N con									
	P con									
	k con			-*						
-W+F	LAR									
	R/S									
	RWC									
	RC	*								
	Chl a/b	*					**			
	N con				*					
	P con				*					
	k con									
+W-F	LAR									
	R/S									
	RWC				*					
	RC									
	Chl a/b									
	N con									
	P con			**						
	k con								-**	
-W-F	LAR									
	R/S									
	RWC									
	RC									
	Chl a/b		**							
	N con									
	P con		*				*			
	k con				-**					

** and * indicate that positive correlation was significant at 0.01, and 0.05 probability levels, respectively; -** and -* indicate that negative correlation was significant at 0.01 and 0.05 probability levels, respectively.

fertilization (nutrients not limiting) was greater than between fertilized and non-fertilized in the well-watered treatment (Yin et al., 2009). But Stroup et al. (2003) have suggested that nutrient determines the plant growth even more than water availability does.

The nutrient availability has been found to alter allocation patterns: the values of the parameter root: shoot, decreased in the conditions with fertilization when compared to conditions without fertilization, despite the same watering regimes. These results indicate that supply fertilization treatments could reduce the growth of roots as well as promote the growth of shoots, especially the growth of leaves. Water or nutrient stress alone did not alter seedling root/shoot ratio, nutrient stress alone had less effect than water stress on this trait, but the com-

ination of water and nutrient stress significantly increased the root/shoot ratio. It was consistent with the report by Stark (1992) and Zainudin et al. (2003), which suggested that simultaneous water and nutrient had the greatest impact on root/shoot ratio. Plant modification of physiological traits such as RWC, leaf relative conductivity, and Chlorophyll a/b are the earlier response to stress environment than plant growth. As shown in Table 2, the results show that RWC and Chlorophyll a/b decreased with the water stress in both fertilizer supply and without fertilizer supply conditions, while the parameter, leaf relative conductivity decreased under the fertilizer supply only under well-watered conditions but greatly increased under water-stressed conditions. Similar results were also reported by previous studies (Legros et

al., 2009; Song et al., 2010; Sanchez et al., 1983; Correia et al., 1989; Marulanda et al., 2010; Li et al., 2010; Yousfi et al., 2010). When the treatment was observed up to 60 or 90 days, our result showed that RWC and Chlorophyll a/b was significantly lower and leaf relative conductivity was significantly higher in water-stressed treatment than in the well-watered treatment, but it increased with nutrient supply. This indicated that water stress applied separately had more effect than nutrient stress on these three traits.

It is shown in Table 3, that at the end of the experiment, water and nutrient stress decreased leaf nitrogen and phosphorus concentration but increased potassium concentration compared to the control treatment ($P < 0.05$); the combination of water and nutrient stress made significant effects on nitrogen and phosphorus concentrations, but there was no significant difference between the control and the potassium concentration. Many studies have been carried out to indicate that water deficit reduced N and P concentrations in leaves; N and P were affected more than K and plant nutrient content were lower under drought stress and soil nutrient shortage and overdose; their findings are in accordance with the present results (Eck and Musick, 1979; Shanguan et al., 2000; Bruyn et al., 2002). It can be seen from Table 4 that the more significant correlations between leaf area, root/shoot ratios, Chlorophyll a/b and phosphorus concentration with other index under different treatments than other investigated traits, may be good indicators for the physiological and growth characters, nutrient concentration responses to water and nutrient stress of oil palm seedlings.

In conclusion, the growth, biomass partitioning, nutrient concentration and the morphological and physiological properties of oil palm were affected by water and nutrient availability, but it appeared more affected by water stress. Fertilization under well-watered conditions alleviated the nutrient stress, while fertilization under water-stressed conditions aggravated the drought stress, by dissolving the fertilizer. The result also suggests that water \times nutrient interaction had the greatest influence on changes in these traits of oil palm.

ACKNOWLEDGEMENT

The work is jointly supported by the Central Public-interest Scientific Institution Basal Research Fund (ITBKF081), Feasibility Analysis of Development of Oil Palm and Tea-oil Tree Industry (2010-YBJ-03), One Hundred-Talent Plan of Chinese Academy of Sciences (CAS), the CAS/SAFEA International Partnership Program for Creative Research Teams, the National Natural Science Foundation of China(41171216), the Strategic Priority Research Program of the Chinese Academy of Sciences(CAS)(XDA01020304),Yantai Double-hundred Talent Plan(XY-003-02) and the Science and Technology Development Plan of Yantai City (2011016).

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